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EXPERIMENTALLY DEMONSTRATED ECHOLOCATION IN THE AMAZON RIVER PORPOISE, INIA GEOFFRENSIS (BLAINVILLE)

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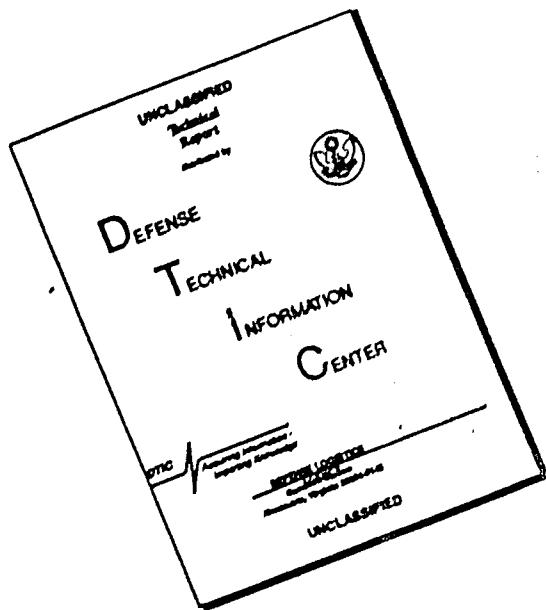
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Work was performed under UF12-523-101, NAVORD, by members of the Marine Bio Science Division. Work was performed from March 1969 to December 1969.

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The assistance of P. Tyron for his illustrations and L. Skinner for her patience and typing is acknowledged.

This revision of NUC TP 187 corrects errors in the original version. It is requested that all copies of the original report be destroyed.

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SUMMARY

PROBLEM

Investigate echolocation and related behavior in the Amazon River porpoise, *Inia geoffrensis*. Experimentally demonstrate biological sonar within the context of operant conditioning.

RESULTS

1. The 50 percent threshold of detection for copper wire by echolocation was found to be 1.12 mm diameter at 19 cm from the tip of the rostrum.
2. The *Inia*'s click trains ranged from 25 to 200 kHz; major energy was centered around 100 kHz.
3. The longest periods of silence for the *Inia* were 8 sec.
4. Corollary behavior exhibited during the performance of the conditioned task indicated a two-step sonic appraisal of the stimulus condition.

RECOMMENDATION

Acoustic contamination in the form of bubble accrual on stimulus displays must be accounted for in echolocation studies.

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INTRODUCTION

Although biological sonar is now assumed to be part of the sensory repertoire of all small odontocete cetaceans (Dudok van Heel, Ref. 1), few have demonstrated this ability in an experimental situation. Only three marine species of the family *Delphinidae* have been the subjects of rigorous experimental paradigms demonstrating functional echolocation. Of the eight studies reported (table 1), six used the bottle-nose porpoise *Tursiops truncatus* Montagu as subject animals: these are probably the most thoroughly studied, observed, and displayed of all captive cetaceans (Ridgeway, Ref. 2). In contrast, river porpoise *Inia geoffrensis* (Blainville) were first observed in captivity in 1956 (Layne and Caldwell, Ref. 3) and displayed in 1962 (Curtis, Ref. 4).

Considered the most primitive of living odontocete cetaceans (Simpson, Ref. 5), the family *Platanistidae* consists of four riverine genera, each containing one species; two old world forms, *Platanista gangetica* (Lebeck) and *Lipotes vexillifer* Miller and two new world forms, *Pontoporia blainvilliei* (Gervais) and *Inia geoffrensis* Layne (Ref. 6) suggested possible echolocation in *Inia* while definitely noting acute underwater hearing.

The first proposed investigation of echolocation in *Inia* was initiated by Phillips and McCain (Ref. 7). Their initial observations were that vision, rather than echolocation, was used to locate objects. As a result, a black and white visual discrimination study followed; this study is presently the only published data on visual discrimination in *Inia geoffrensis*.

Caldwell, Caldwell, and Evans (Ref. 8), while reporting a preponderance of low-frequency, low-energy phonations, found evidence of pulsed sounds, ranging up to 110 kHz, which resembled echolocation. Because of instrumental limitation, these high-frequency pulse trains were considered suspect, although they did point out the possibility of high-frequency echolocation in *Inia*.

Penner and Tusnoda (Ref. 9), reporting preliminary results of conditioned behavior and echolocation in *Inia*, found demonstrable evidence of functional biological sonar. Two male *Inia* from the Orinoco River were conditioned using operant techniques to respond to the presence or absence of a metallic disk suspended behind an optically opaque, acoustically transparent screen. Monitoring *Inia* phonations in the auditory ranges proved to equal the previously reported dearth of sonic activity (Ref. 8). However, use of electronic gear, which translated high-frequency acoustic activity downward into the audio range, gave dramatic evidence of continual pulsed sonic activity. Both Orinoco River *Inia*, after 30 days of conditioning, were responding correctly at the 85 percent level. A tape recording was made using an Ampex FR 1300, an Atlantic Research Corporation LC 32 hydrophone, and a solid-state amplifier (frequency response, 50 to 500 kHz). Analysis of tape segments by the Dynamic Analysis Branch, PMR, Point Mugu, using a Brüel and Kjaer one-third octave analyzer (0 to 40 dB), indicated pulse trains with very little energy below 16 kHz (-33 dB full scale); the major energy was around 64 kHz (-5 dB). Pulse repetition rates in the segments analyzed averaged 50 per second. Pulse energy, indicated at 128 kHz (-25 dB), was questionable because of hydrophone limitation at these frequencies.

The empirical research reported in this paper comprises quantitative and qualitative demonstrations of echolocation in: *Inia geoffrensis*. In addition to salient aspects of acoustic output, collateral and general behavior is noted.

Table 1. Experimental Studies Demonstrating Functional Echolocation in *Delphinidae*

Reference	Date	Species	Method of Determination	Method of Vision Exclusion
Berta (ref. 10)	Manuscript State	<i>T. truncatus</i>	Operant conditioned Shape discrimination	Suction eye cups
Busnel and Dziedzic (ref. 11)	1966	<i>Phocaena phocaena</i>	Avoidance maze	Suction eye cups
Evans and Hall (ref. 12)	MS	<i>Lagenorhynchus obliquidens</i>	Operant conditioned Plate discrimination	Acoustically transparent, visually opaque screen
Evans and Powell (ref. 13)	1966	<i>T. truncatus</i>	Operant conditioned Plate discrimination	Suction eye cups
Johnson (ref. 14)	1966	<i>T. truncatus</i>	Operant conditioned Object location	Suction eye cups
Kellogg (ref. 15)	1961	<i>T. truncatus</i>	Avoidance maze	Turbid water Darkness
Norris, et. al. (ref. 16)	1961	<i>T. truncatus</i>	Avoidance maze Objection location	Suction eye cups
Turner and Norris (ref. 17)	1966	<i>T. truncatus</i>	Operant conditioned Sphere discrimination	Suction eye cups

MATERIALS AND METHODS

Experimental Subject

The subject animal of this study was a male *Inia geoffrensis* captured in the Solimoes section of the upper Amazon near Leticia, Colombia, during early May 1966. The animal (designated 139-I.G.-8) was flown, via Florida, to the Naval Undersea Research and Development Center, Point Mugu, California, and was placed in a fresh water holding tank for 2 weeks. He was then flown to the Naval Undersea Research and Development Center's Hawaii Laboratory at Kaneohe Marine Corps Air Station on the island of Oahu, Hawaii.

Layne (ref. 6) observed individual *Inia* approximately 9 ft long in the field. Thus, because the I.G.-8 was 5 ft long (155.1 cm from tip of rostrum to fluke notch), he was apparently subadult. His weight, upon arrival in Hawaii, was 39.9 kg, increasing to 43.5 kg during 9 months of captivity.

The *Inia* was fed ($\bar{x} = 1.440$ kg = 3.3 percent of body weight/day) a mixed diet of pompano (*Palometa simillima*), pacific mackerel (*Pneumatophorus diego*), and night smelt (*Spirinchus starksii*).

Initially, the animal was daily given 1250 mg of tetracycline by food-embedded capsules. This dosage was later reduced to 750 mg and eventually eliminated.

Tank

A circular aluminum-plastic tank (fig. 1) was located within a link chain enclosure on a wooden platform 46 cm above ground. This enclosure was protected from rain and direct sunlight by a corrugated metal roof approximately 3 m above the tank. The tank was 7.3 m in diameter, and 1.2 m high. A garden hose delivered 65 l/min of fresh water into the tank. Water level was maintained by a drain opening in the tank's side at 1.1 m. At this level, the tank contained 44,835 l of water.

Tank water temperature ranged from 21.1°C to 24.7°C. Air temperature was from 17.8°C to 30.0°C. Water chlorine content was maintained at approximately 0.2 ppm by constantly dripping dissolved sodium dichloro-a-triazinetrione into the tank from a 20-l container.

Conditioned Task

The *Inia* was conditioned to hold position at the station area near the side of the tank. Upon the introduction of a 1-sec burst of 30-kHz sound generated by a Hewlett-Packard oscillator through a Clevite CH-15J hydrophone, he was expected to turn and swim toward the visual screen of a target area apparatus. If he detected a target behind the visual screen, he swam to a "yes" manipulandum and activated it. If no target was present, he was trained to swim to a different manipulandum and trip it.

The total number of training trials required from initiation of training to the *Inia*'s attainment of the 90.0 percent correct response level with the largest training target was 1322 ($\bar{x} = 73$ trials/day).

Target Area Apparatus

The target area apparatus (3.3 m X 1.3 m) (fig. 2) consisted of a wooden frame with corrugated (and beaded) aluminum attached as visual shields on both sides of the target area. The target area was fitted with a visual screen (120 cm X 48 cm) (fig. 3) of black, 1.6 mm thick acrylic attached to a wooden frame. The visual screen and its frame were constructed to slide in and out of a slot between the visual shields. The apparatus was attached by C clamps to the tank top; it extended

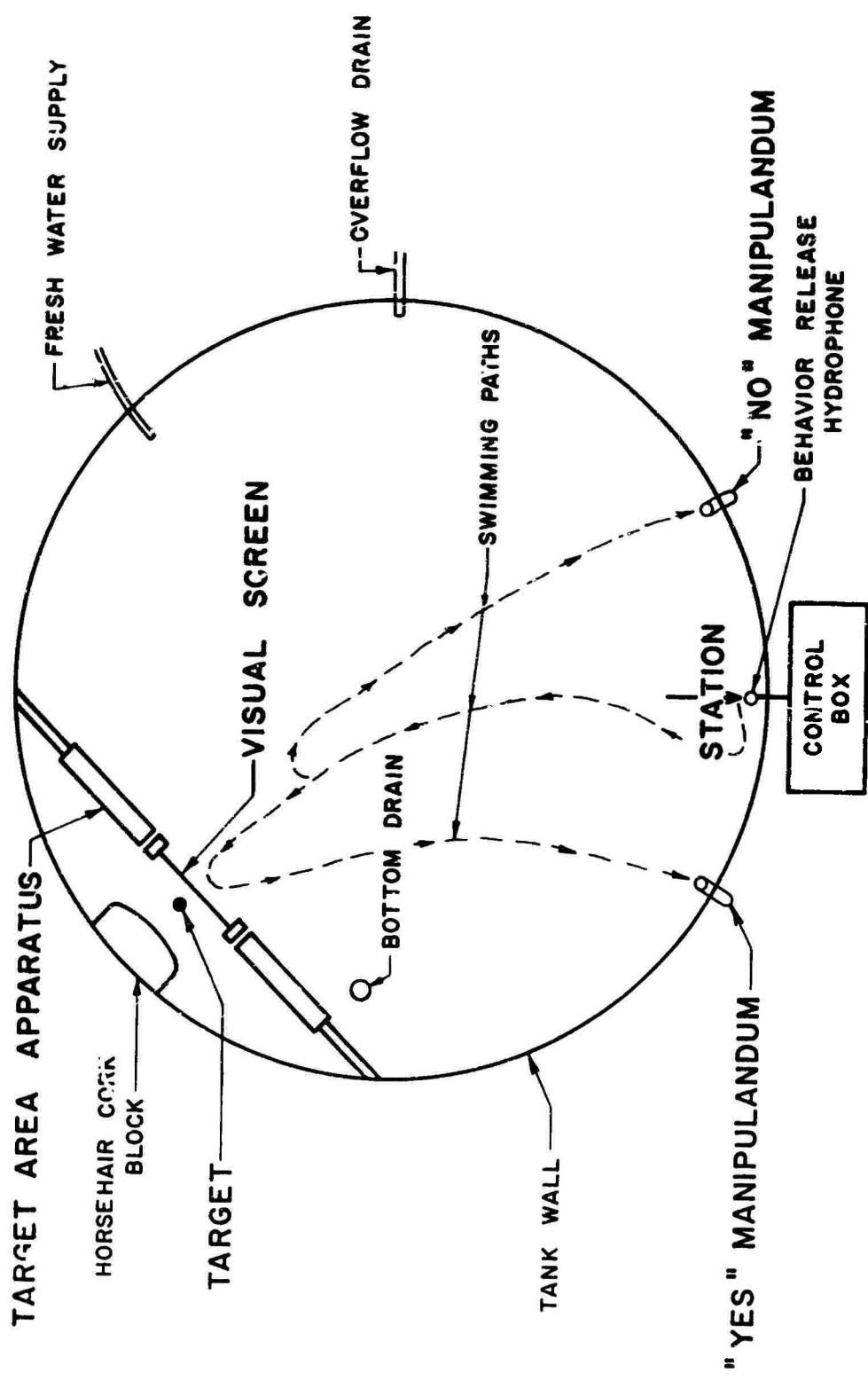


Figure 1. Experimental tank.

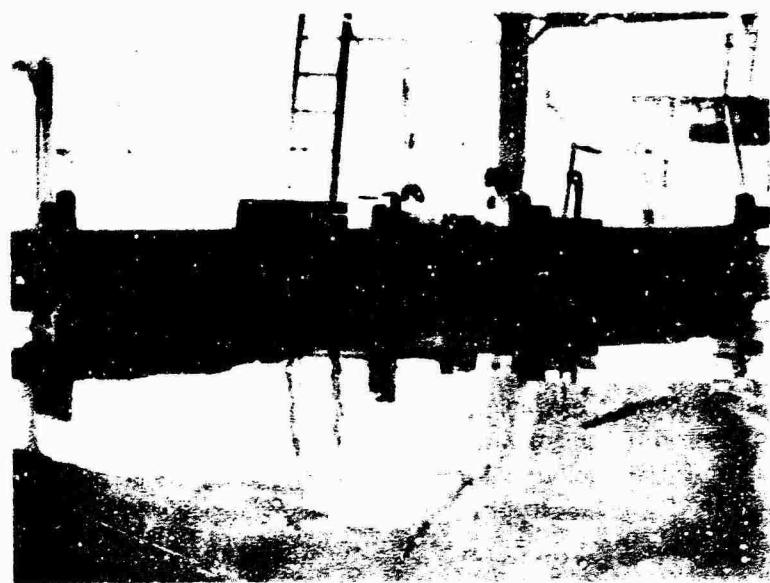


Figure 2. Target area apparatus with visual screen in down position.

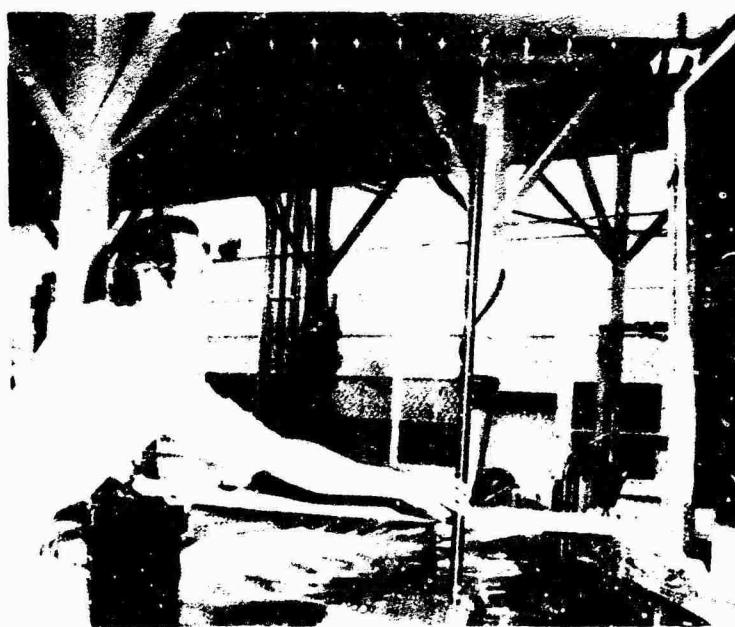


Figure 3. Acrylic visual screen in raised position showing Phase I target and target arm.

from 24 cm above the water surface to the bottom. Between each training or experimental trial, the visual screen was raised by line and pulley, and the target was removed or attached while both visual screen and target were out of water. This method was used to eliminate the possibility of the *Inia* detecting the sound of a target entering or leaving the water because sounds produced by the visual screen and its heavy frame, as they were lowered into the water, were assumed to be the same with as without a target attached.

Directly behind the target area, against the tank wall, was a 125 cm X 64 cm X 25 cm block of rubberized horsehair matte material covered by 1 cm of acoustical cork.

Acoustical Properties of the Visual Screen

K. J. Diercks of the Applied Research Laboratories of the University of Texas at Austin performed transmission measurements on an acrylic sheet identical to the one used as the visual screen in this study. The results of these measurements are given in figure 4. The values reported are for steady-state (narrowband) signal conditions.

The acoustical effects of the visual screen on the target detection ogive were tested by conducting four 30-trial, randomized sessions with the 0.6-mm target. The same procedure used for Phase II* was followed except that the acrylic sheet was removed. These sessions, conducted during daylight without elimination of vision, resulted in only 01.7 percent correct responses for the with-target trials. Comparison with the 0.6-mm target results of the regular experimental sessions (see section on Results) indicated negligible effects on echolocation by the acrylic screen.

Targets

Initial training was conducted utilizing a hollow, seamless, aluminum tube with a wall thickness of 3.05 mm. This cylinder was 3.81 cm in diameter and 107 cm long. It was closed at both ends with wooden plugs, and painted flat black. Training was also conducted utilizing targets of the same material, length, and wall thickness with outside diameters of 3.17, 2.54, 1.90, 1.27, and 0.63 cm. During the first phase of this study, experimental trials were conducted using only the 1.90 and 1.27 cm outside diameter targets.

During the experimental determination of target-diameter detection threshold, 13 copper wires (magnet type R2, A.W.G. #12) were used as targets. These wires were stripped of all insulation and enamel, and soft drawn to diameters ranging from 2.6 to 0.6 mm. Each target wire had a loop at one end, a size-32 rubber band at the other end, and a small paper label. Targets, 105 cm long, were attached to a hook at the bottom of the visual screen and by the stretched rubber band to the top of the visual screen.

*Phase I refers to the experimental demonstration of the *Inia*'s ability to echolocate, and Phase II is the experimental determination of target detection thresholds.

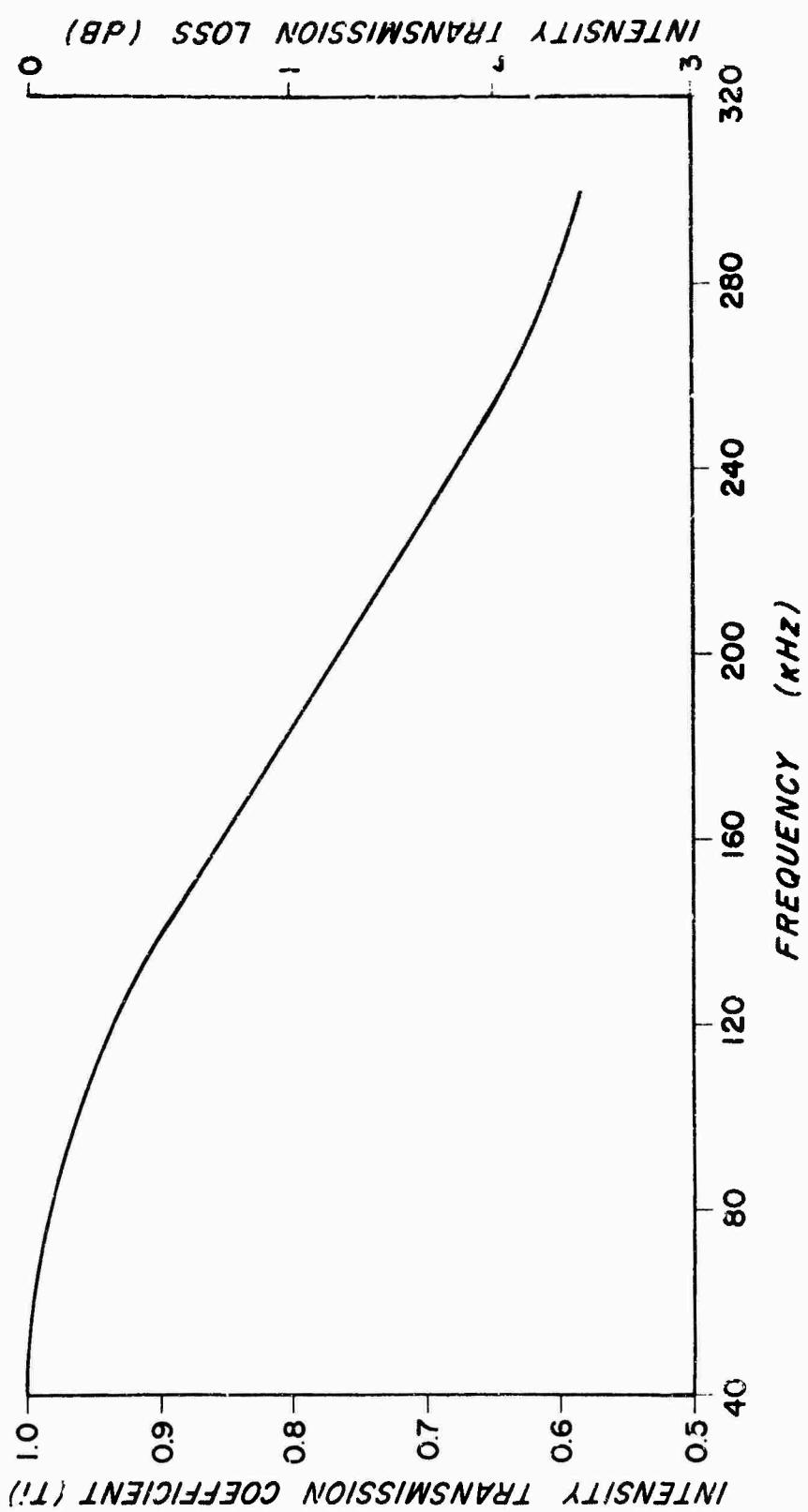


Figure 1. Acoustical transmission characteristics of visual screen. (Courtesy of K. J. Dietrich, Applied Research Lab., University of Texas, Austin.)

Manipulanda

Each of the two manipulanda (fig. 5) consisted of a round (diameter = 1 cm) dowel tipped with a 4 cm length of air-filled plastic tubing attached to a Robert-Shaw Fulton 360° microswitch mounted at the end of a U-shaped conduit. The microswitch was wired to turn a red light mounted in a control box in front of the operator off and to activate a 4-kHz Mallory sonalert device mounted in the operator's control box. The manipulanda were attached by C clamps to the tank wall with the dowel projecting 15 cm into the water – 35 cm from the tank wall.

Experimental Procedures

The presence or absence of a target was randomized for trials within the experimental sessions. Equal numbers of each resulted.

During Phase I, a wooden arm extended back from the top of the visual screen frame. The targets were suspended by a shock cord from hooks on the underside of this arm (fig. 3). The hooks were spaced 10 cm apart, from 24 cm to 114 cm behind the visual screen. A 20-trial session, using the 1.90 cm diameter target, was conducted at each 10-cm increment behind the visual screen starting at 24 cm. This procedure was then repeated with the 1.27 cm diameter target. This gave a total trial number of 400.

Each 20-trial session lasted 30 min with an average of 1.5 min to conduct the trial, record results, raise the visual screen, remove or suspend the target, and lower the visual screen.



Figure 5. IG-8 activating manipulandum.

While determining the target detection thresholds, the conditioned task, target area apparatus, and manipulanda were essentially the same as those used for Phase I except that the target arm extending behind the visual screen was replaced with a shorter arm with only one hook 19 cm behind the screen. Another short arm was attached at the bottom of the visual screen; this arm also had a hook 19 cm behind the screen. The targets were attached at the top and bottom of the visual-screen frame.

To determine the target detection ogive (Phase II) of *I. geoffrensi*, four random sessions of 30 trials (15 with-target, 15 without-target) were conducted using each of the 13 wire target diameters (1560 trials, 780 with-target).

Each 30-trial session lasted approximately 45 min ($\bar{X} = 43.3$) with an average of 1.5 min per trial.

Latencies from the onset of the 30-kHz behavior release signal until the *Inia* activated one of the manipulanda were measured with a hand-held stop watch and recorded for each trial.

Elimination of Bubble Formation

Each target was polished with number-32 crocus cloth and detergent. Immediately prior to each session, the target was thoroughly cleaned of all oxides or other surface irregularities. During sessions, the target was wiped with liquid detergent between trials. No more than 5 sec elapsed before introduction of the 30-kHz behavior release tone after the visual screen and target were lowered. As a further precaution, the tank's fresh water inflow was turned off 1 hr before the session started. The visual screen was also washed thoroughly before each session with liquid detergent.

Two special 30-trial sessions with unpolished 0.8 and 0.6 mm targets were conducted. The same experimental procedures were used except that 1 min elapsed after lowering the visual screen and target into the water before giving the behavior release tone to start the trial. Each special session was repeated with polished 0.8 and 0.6 mm targets with a 5-sec immersion time before trial initiation. The special sessions with the unpolished targets and 1-min delay after target immersion resulted in 100.0 percent correct responses with the 0.8-mm target and 93.3 percent correct responses with the 0.6-mm target. Bubble-formation elimination procedures used in the repeated special sessions resulted in 13.3 percent correct responses with the 0.8-mm target and 0.0 percent correct responses with the 0.6-mm target. Both of these special sessions ($N = 30$ each) agree closely with the values reported in table 4 ($N = 120$). The correct-response percentages of the with-target trials clearly illustrate the necessity of bubble-elimination measures.

Phonation Monitoring Equipment and Procedures

Instrument systems used to obtain frequency profiles and 24-hr phonations are in figure 6; basic instrument information is in table 2.

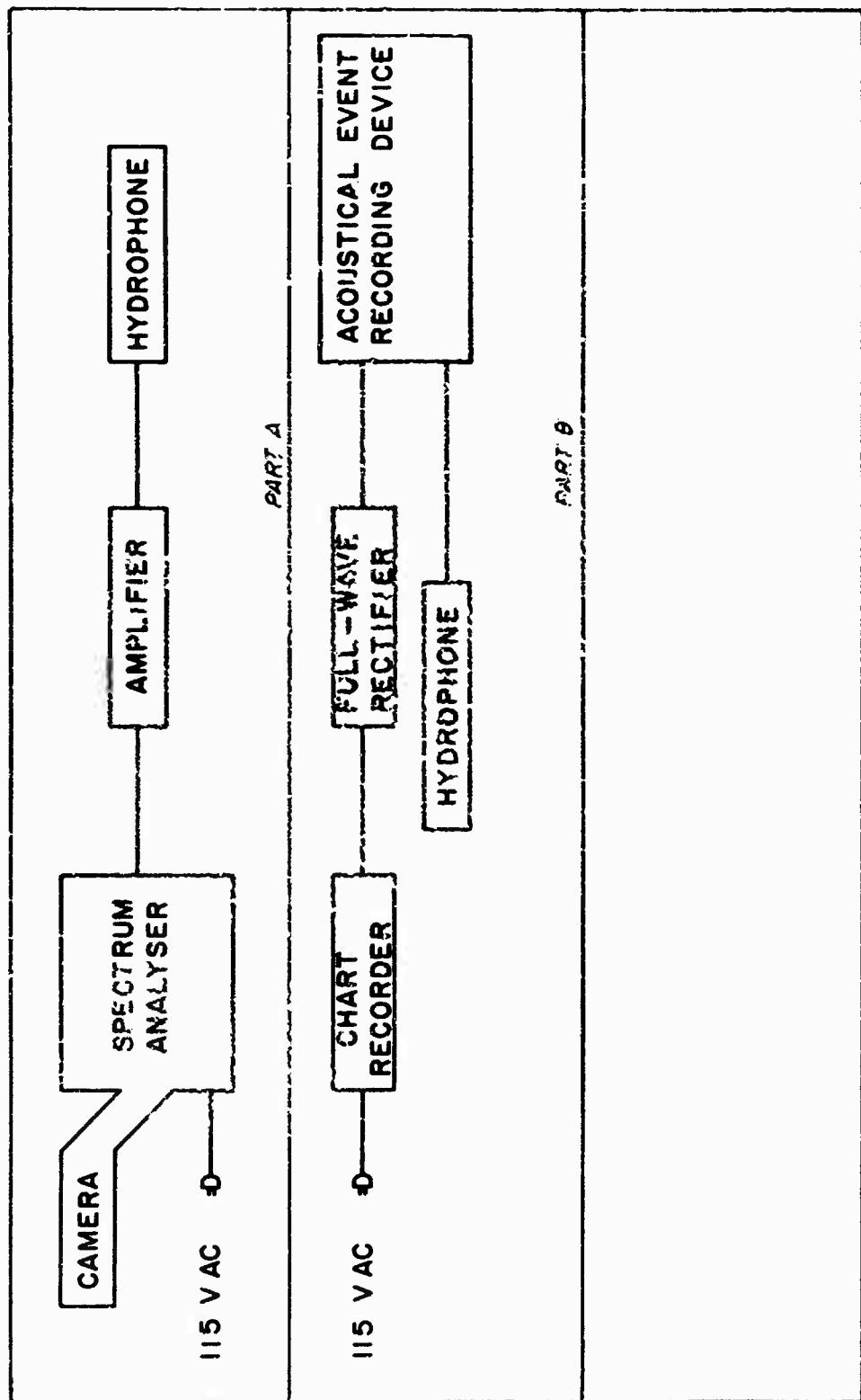


Figure 6. Block diagrams of instrumentation. Part A: Instrument system used to obtain frequency profiles. Part B: Instrument system used for 24-hr phonation monitoring.

Table 2. Phonation Monitoring Instrumentation information

Figure	Instrument	Make	Model	Settings of Specifications
Part A of figure 6	Spectrum analyzer	Tektronics	Type 3LS	0.5 v/div 0.50 msec/div
	Amplifier	Hewlett-Packard	466A	40 dB
	Hydrophone	Atlantic Research Corp.	LC-10	0 to 120 kHz
Part B of figure 6	Acoustical event device	Aquasonics	S420	Broadband
	Full-wave rectifier	In-house		
	Chart recorder	Mosely		Chart speed = 2 in./min
	Hydrophone	Aquasonics	TD-420	Tuned ceramic cyclinder

During 72 periods of frequency-profile monitoring, the hydrophone was suspended approximately 30 cm in the water near the tank's side or from the target hook behind the visual screen. The frequency profiles recorded while the hydrophone hung in the water, in place of a target, were obtained by conducting target detection trials with the same procedures used in previously described experimental sessions.

One 24-hr phonation period was recorded with the hydrophone suspended approximately 15 cm into the water at the center of the tank. The Aquasonics acoustic-event indicating device and chart recorder were turned on and left to operate in the absence of anyone in the tank area.

Methods of Observation

Miscellaneous diurnal behavior observations were made opportunely from both above and beneath the water surface. Lighting conditions precluded dependable nocturnal observations.

Breathing rate observations of 15 min were timed with a hand-held stop watch, starting at the moment of the first breath. Breathing rates were taken randomly during daylight hours for 187 days.

RESULTS AND OBSERVATIONS

Phase I – Demonstration of Echolocation

The results of the first phase of this study are summarized in table 3. Chi square and probability values given are for "with" and "without" target trials combined.

Table 3. Results of Trials with 1.90 and 1.27 cm Diameter Targets (Phase I)

Target Diameter	Percentage of Correct Responses			N	χ^2	P
	Target	No Target	Total			
1.90 cm	97.0	99.0	200	200	184.4	<0.001
1.27 cm	95.0	95.0	200	200	162.0	<0.001

Phase II – Determination of Detection Thresholds

Table 4 summarizes the results of wire-detection trials. The percentages given are the mean percentages of correct responses for four sessions with each target diameter. Thus, each percentage is based on 60 trials (15 with target per session and 15 without target per session). Standard deviations of the means are based only on with-target trials.

At target diameters having less than 100.0 percent correct responses for with-out-target trials, the percentages of correct responses for with-target trials were corrected for chance success. This correction was calculated utilizing a method given by Green and Swets (ref. 18). This method has as its basis the statement

$$\text{corrected } P(T/t) = \frac{P(T/t) - P(T/n)}{1 - P(T/n)},$$

where $P(T/t)$ is the probability of correct with-target responses and $P(T/n)$ is the probability of incorrect without-target responses.

Utilizing a frequency method suggested by Woodworth and Schlosberg (ref. 19), the mean percentages of correct responses for with-target trials (table 4) were plotted against target diameters and an ogive hand fitted through them (fig. 7). The traditional 50 percent correct-response-level threshold is estimated by the plot as 1.12 mm copper wire. An estimate of the 25 percent correct-response-level threshold is 0.96 mm, and the 75 percent correct-response-level threshold is 1.32 mm by this ogive.

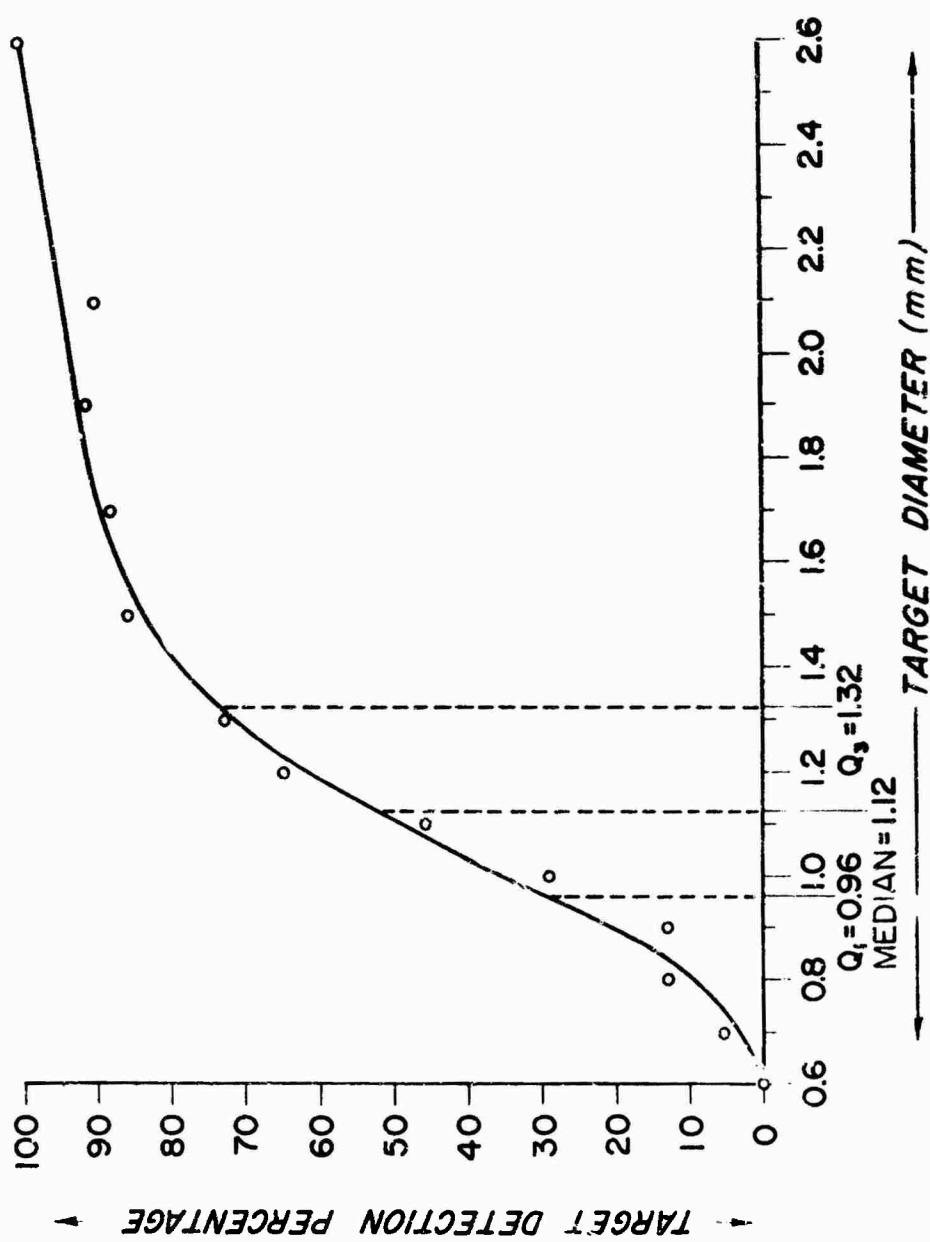


Figure 7. Ogive of *Intia gossensis* wire-detection thresholds (Phase II). $Q_1 = 25$ percent correct response threshold; median = 50 percent correct response threshold; $Q_3 = 75$ percent correct response threshold.

Table 4. Results of Wire-Detection-Trials (Phase II)

Target Diameter (mm)	Correct Response Percentages			SD*
	Target Trials (Corrected)	No Target Trials		
2.6	100.0	100.0		0.0
2.1	90.0	100.0		10.0
1.9	91.7	100.0		10.0
1.7	88.3 (87.2)	91.7		13.2
1.5	86.0 (85.3)	95.0		11.4
1.3	73.3	100.0		5.0
1.2	65.0	100.0		5.4
1.1	48.3 (44.6)	93.3		16.7
1.0	35.0 (29.0)	91.6		10.9
0.9	13.3	100.0		9.4
0.8	15.0 (13.5)	98.3		22.0
0.7	05.0	100.0		3.3
0.6	0.0	100.0		0.0

* SD = standard deviation of session means (with-target trials only)

Results of Phonation Monitoring

Relevant acoustic activity or click production in *Inia* is restricted to ultrasonic broadband emissions. Whistles or pure tones were absent as previously reported by Caldwell, Caldwell, and Evans (ref. 8). The click trains decayed rapidly below 40 kHz and were rarely seen below 25 kHz. Major areas of energy occurred between 70 kHz and 170 kHz (figs. 8 to 10).

A monitored 24-hr period of acoustic activity (fig. 11) indicated three rather distinct density periods. Because silent times were not longer than 5 sec and because these occurred in the low-density period, no acoustic discontinuity is indicated in figure 11. The lowest density periods occurred between 0300 and 0800 hours. Two periods of middle density acoustic activity occurred: the first between 0800 and 1200, the second between 1900 and 0300. The period of most intense acoustic activity was between 1200 and 1900.

The acoustic activity reported in this paper agrees with a normal day of training or testing and may, as Powell (ref. 20) suggests, reflect the captive discipline and environment.

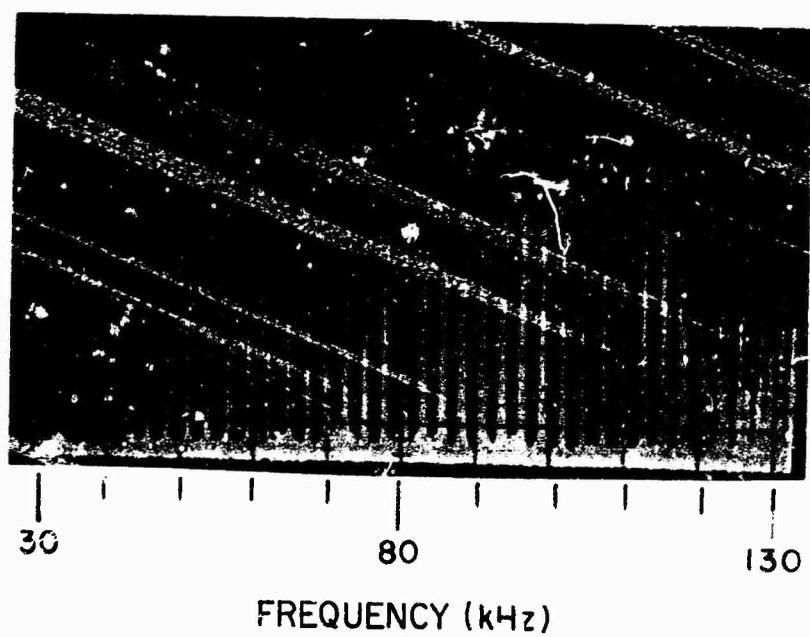
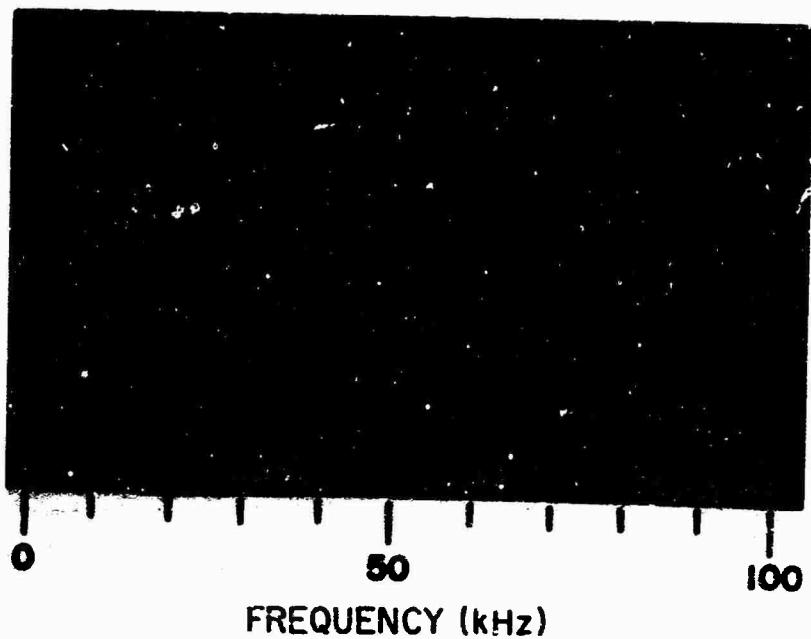


Figure 8. Spectrum analyzer traces of typical *Inia geoffrensis* phonations.
Part A: Center frequency = 50 kHz. Part B: Center frequency = 80 kHz.

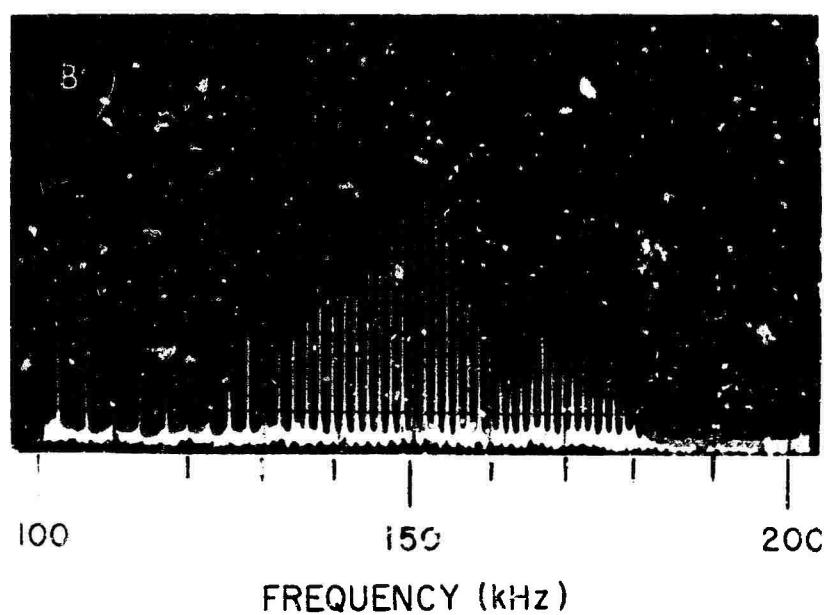
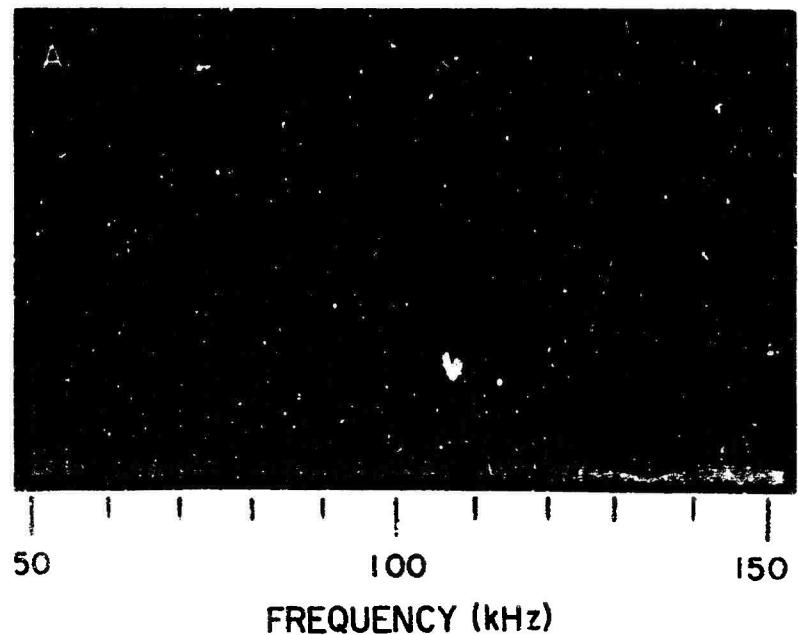


Figure 9. Spectrum analyzer traces of typical *Inia geoffrensis* phonations.
Part A: Center frequency = 109 kHz. Part B: Center frequency = 150 kHz.

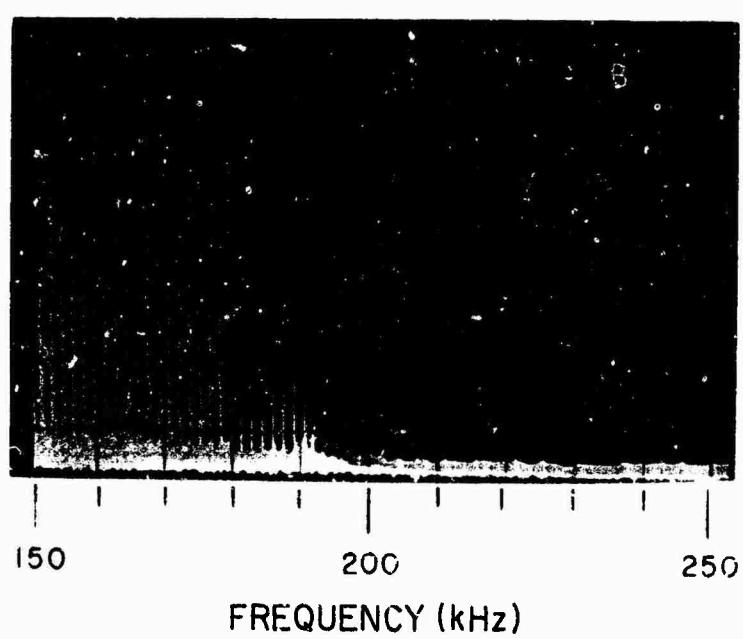
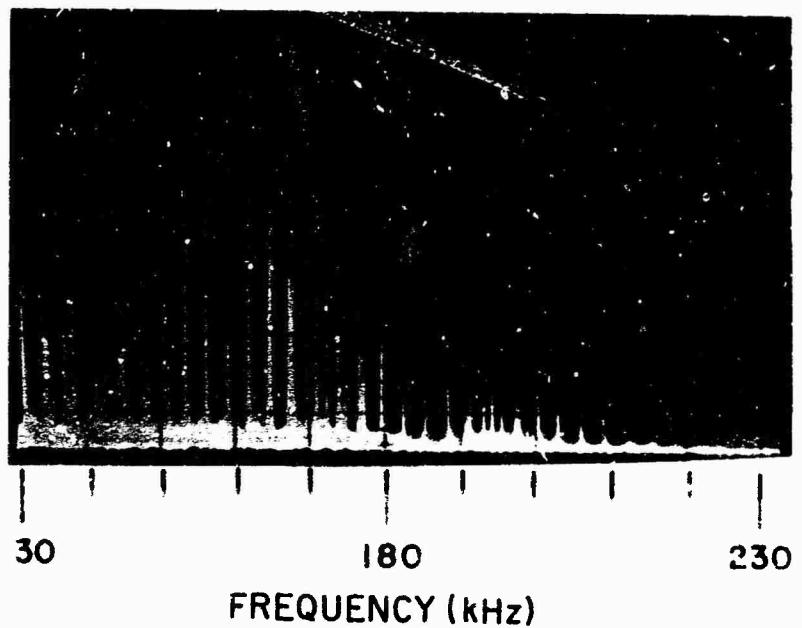


Figure 10. Spectrum analyzer traces of typical *Inia geoffrensis* phonations.
Part A: Center frequency = 180 kHz. Part B: Center frequency = 200 kHz.

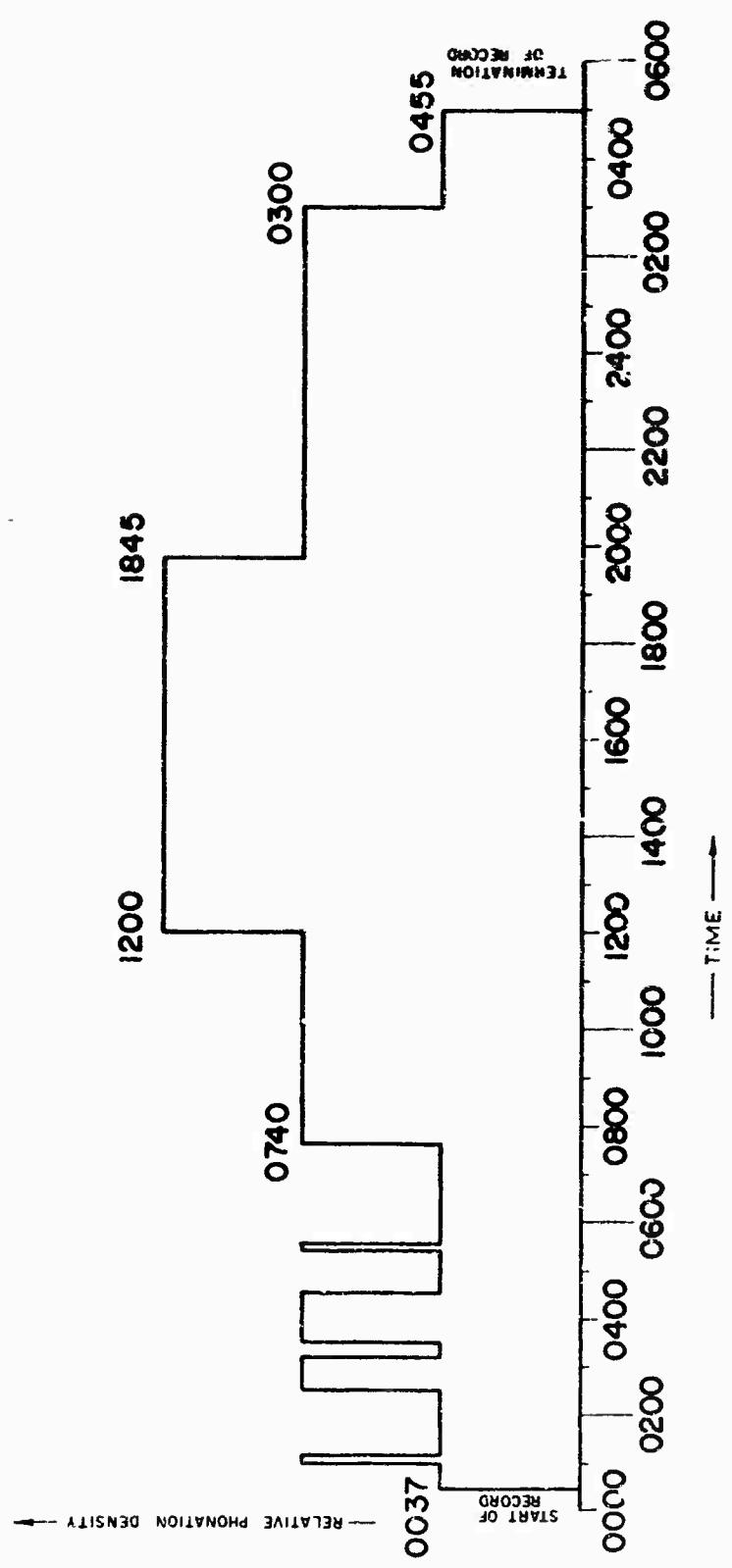


Figure 11. Results of 24-hr monitoring of IC-8's phonations showing times of occurrence of three relative levels of density.

Behavior Observations

As a result of mounting the response manipulanda away from the stimulus display, a number of informative collateral behaviors were generated, and the presence of others were not obscured. The manipulanda, essentially "yes" and "no" in this context, were mounted on the wall opposite the stimulus display. The station for IG-8 was the area between the manipulanda, facing the experimenter.

When the stimulus display first touched the water, IG-8 came to station, generally resting the tip of his right pectoral flipper and the trailing edge of his flukes on the bottom.

Onset of the behavior release tone resulted in a back-flip turn and a direct run to the stimulus display. In difficult with-target trials, the total distance was traversed to acrylic screen with contact, hesitation, and rotation of head and body oriented in the plane of the vertical stimulus wire. During these trials, IG-8 would generally exhibit a jaw gape at approximately a 90° rotation of the body from its normal position. The jaw gape reported by Layne (ref. 6) resembles the behavior seen in IG-8. Jaw snapping and yawning were not rare in IG-8, and differences between these three behaviors were distinct. Larger stimuli resulted in a shorter travel distance to the stimulus display by IG-8. In extreme cases, the initial flip turn from the station toward the stimulus display was abruptly followed by another flip turn to the response manipulandum occurring within the body length of IG-8.

In all cases, the abruptly terminated runs were associated with no-stimulus determinations, positive or false. A closer scrutiny was always elicited when stimuli were detected as present. The behavior elicited by the no-stimulus presentation was directly related to size or ease in detecting the stimulus being tested in that session. Easy stimulus detection sessions resulted in rapid appraisal of both cases; however, there were consistently shorter latencies in the no-stimulus trials. Difficult stimulus sessions demonstrated the same latency relationship although both were lengthened.

Postponed or secondary vicarious trial and error occurred on return from the stimulus display to the response manipulanda. Exaggerated and abrupt changes in direction or vacillation at midpoint of return were noted in the smaller stimuli sessions.

Auditory scanning (Kellogg, ref. 21; Norris, et. al., ref. 16) was noted in *Inia* by Layne and Caldwell (ref. 3) as possible evidence for echolocation. Auditory scanning demonstrated by IG-8 as well as by the two Orinoco River *Inia* (Penner and Tsunoda, ref. 9) is distinguished from that of *Tursiops* by rectangular scanning adjustments. Norris, et. al. (ref. 16) and Evans and Powell (ref. 13) describe lateral swinging or circular head movement in auditory scanning. In contrast, *Inia* apparently make discrete linear adjustments horizontally and vertically with abrupt right-angle transitions.

During this study, several behavioral observations were made. These observations were other than those related to aspects of the conditioned task.

Previously reported *I. geoffrensis* behaviors such as upside-down swimming (Layne and Caldwell, ref. 3), snorting (Layne, ref. 6), and food manipulation (Layne and Caldwell, ref. 3) were essentially the same with IG-8. Observations of IG-8

indicated that upside-down swimming, very near the bottom with the melon often touching, was primarily an appetitive behavior, and that snorting, in addition to mucous expulsion, may in part be related to a "frustration" or "annoyance" like stress. Food manipulation by IG-8 was usually with the left side of his mouth. He showed a preference for pompano with the heads removed and the tails remaining. If given a fish with the head intact, he usually either bit off or broke it off by holding it distally between the jaws with the fish head against the tank bottom and twisting his head and/or body. If given a pompano with the tail removed, he would often drop it and leave it on the bottom, usually eating it later.

Surfacing for breath was accomplished in the usual slow ascent manner or faster body-roll fashion described by Layne (ref. 6). Within the human hearing range, both expiration and inspiration were extremely quiet — more quiet than for other porpoises which are familiar to the authors. Breathing rate observations yielded a mean of 1.44 breaths/min (95 percent confidence interval: 1.07 to 1.81 breaths/min).

The *Inia* were observed lying motionless on the bottom on several occasions. The longest of these periods was 35 sec. This motionless lying and the following behavior were observed only when the experimenter was hidden and motionless on a platform above and at the side of the tank with the *Inia* apparently unaware of his presence. Immediately following some motionless periods, and after surfacing to breathe, IG-8 would stop swimming and slowly flex the posterior part of his body downward until it was almost at a 90° angle with his flukes held horizontally (parallel with the anterior portion of his body). He would hold this position approximately 3 sec and then flex the posterior part of his body to almost the same angle upward from the rest of his body, but with the flukes held vertically (in line with the flexed posterior part of his body). This position was held for 2 to 3 sec, and then normal swimming motions were resumed. It appears that this behavior belongs to the category of behavior termed "comfort movements."

On three occasions, wrinkling of the anterior surface of the *Inia*'s melon was observed. This was seen as small, shallow wrinkles radiating dorsally and laterally from the midpoint of the transverse groove between the melon and the rostrum. These wrinkles were less distinct approximately 3 cm from the point of radiation, becoming invisible approximately 5 cm from that point. They curved slightly toward the midline near their ends giving a slight open circle appearance to their pattern. They were observed for only a few seconds each time. Unfortunately, they could not be photographed.

DISCUSSION

Exclusion of visual information, a major concern in delphinid echolocation studies, is compounded in *Inia* by the addition of probable tactile specialization (Layne and Caldwell, ref. 3). This unique occurrence of rostrum vibrissae (ref. 3) in an adult cetacean and of observed manipulative behavior necessitates exclusion of this modality also.

The physical, optical, and acoustic properties of opaque acrylic sheets met experimental requirements and greatly simplified the necessary conditioning. In naive subjects, a month or more may be needed to condition behavior involved in putting on and removing suction eye cups. Suction eye cups, now an accepted tool in cetacean psychophysics, were first used by Norris *et. al.* (ref. 16) in their incisive demonstration of echolocation in *Tursiops truncatus*. The design suggested by F. G. Wood (ref. 22) ruled out vision, obviating the use of dyes, turbidity, or darkness which had previously been the alternative to surgical destruction. In addition, these methods seriously curtailed the observation of subjects being tested.

Kellogg (ref. 15) used a clear plexiglas/acrylic sheet to demonstrate *Tursiops* echolocation related to barrier avoidance in turbid water. Schusterman (ref. 23) described a target of air sandwiched between acrylic disks. The air-water interface is calculated to be an excellent acoustic reflector (Parvulescu, ref. 24).

Kellogg and Rice (ref. 25), in a visual discrimination study, used clear plexiglas to cover underwater stimulus patterns, ostensibly ruling out echolocation. The stimulus forms of thin brass were painted flat black, and the figures were cut in stencil fashion. The underwater display thus presented a black-painted, brass form with voids of various shapes behind, and apparently in contact with, the 1/8-in. plexiglas window. White plates were placed behind the figures to give a visual contrast. Based on empirical work with acrylic sheets in stimulus detection and discrimination by echolocation – reported in this paper – the results of the visual discrimination study by Kellogg and Rice can be interpreted to reflect an unknown but appreciable amount of discrimination by echolocation. The description of auditory scanning considered by Kellogg and Rice to indicate lack of evidence for binocular stereoscopic vision could have been the behavior of a porpoise demonstrating a preferred sensory modality in an ambiguous test situation. Thus, evidence suggests that echolocation was dominant, and was as appropriate to the method of presentation as was the echolocating response similarly evoked from *Inia*. Kellogg's and Rice's observation that lack of scanning behavior in the air test could account for poor test performance was appropriate, regardless of the inference taken. In the absence of ultrasonic monitoring (ref. 25, p. 753), it can only be speculated as to what the acoustic/visual discrimination relationship was.

Wire avoidance thresholds in *Phocaena phocaena* Linnaeus, reported by Busnell and Dziedic (ref. 11), is of interest because it is the only other study related to discrimination of fractional wavelength diameter wires by porpoise echolocation. The threshold of detection in *Phocaena* is substantially lower than that found in *Inia*. Compounding the mystery are the low frequencies reported for *Phocaena* – approximately 2 kHz. Our data indicate that, despite the higher frequencies found in *Inia* echo pulses (100 kHz), the 50 percent level of stimulus detection will fall near 1.1 mm of copper wire. Although the minimum distance (19 cm) to a stimulus wire, imposed by the acrylic sheet, makes direct comparison difficult, the disparity in thresholds between *Phocaena* and *Inia* is probably the function of a previously unreported variable.

The probable unknown first appeared when data fluctuated widely on wire sizes below 1.0 mm. As a result of a warm-up series where errors required time-out periods, a relationship between length of stimulus emersion and correct response was noted. The unknown variable was known, but not realized; bubble deposits were cleared from the screen on each trial; hydrophones were dipped in wetting agents to

postpone bubble deposition. However, the implication that a stimulus wire could be greatly modified in a very short period of time, by an invisible film of gas, was not obvious.

The unknown variable, actually a complex of interrelated variables, had as its basis bubble formation (as a function of time), entrained gas, and seeding site.

To demonstrate the relationship of bubble formation and apparent threshold in wire discrimination, time and wire-surface conditions – the most easily controlled of the complex – were varied during four special sessions. A time of 1 min, measured from the point at which the screen and stimulus wire came to rest in the underwater position, was to be the time allowed for bubble buildup on the stimulus wire.

The resulting 100 percent (0.8-mm target) and 93.3 percent (0.6-mm target) correct responses, corollary behavior, and latency indicated that the subject was having no trouble in stimulus/no-stimulus determinations. However, when the stimulus wires were cleaned with detergent and 5 sec was imposed between stimulus emersion and behavior release, the resulting 13.3 percent and 0.0 percent correct responses, as well as the corollary behavior and latency, indicated a difficult task problem. Another special session with varying behavior release times indicated that under the conditions of this experiment, 35 sec were sufficient for the contaminated 0.8-mm stimulus to approximate 2.6-mm in response and corollary behavior.

The rate of bubble formation under the conditions given was such that at 35 sec, when radical behavior changes were obvious, the bubbles were not visible. At 50 sec, individual bubbles could be seen on the stimulus wire.

Pumps, filters, and heaters will almost invariably generate large amounts of captive gas, seeking equilibrium, and unless extreme caution is exercised to avoid bubble formation, acoustic contamination will render discrimination results questionable.

CONCLUSIONS

1. *Inia* possess biological sonar utilizing click trains with major energy centered at approximately 100 kHz with an overall range of 25 to 200 kHz.
2. The 50 percent threshold of detection for copper wire is at a diameter of 1.12 mm, 19 cm from the rostrum tip.
3. *Inia geoffrensis* is rarely silent; the longest periods of silence recorded were 8 sec.
4. Acoustic contamination in the form of bubble accrual on stimulus displays must be accounted for in echolocation studies.
5. Visually opaque, acoustically near-transparent acrylic screens have been demonstrated to be valid additions to echolocation psychophysics. In the comparative test to establish functional difference caused by the interposed acrylic screen, IG-8 did not manifest significantly improved stimulus detection in its absence.
6. Corollary behavior indicates a two-step sonic appraisal of the stimulus condition, a relationship present from the largest to the smallest stimulus. The first sonic appraisal at a distance resulted in a determination of the presence or absence of

stimuli. Absence of stimuli was reported directly from the point of detection; this point decreased in distance to stimulus display as the stimulus diameter was decreased. The second more cautious "with stimulus" sonic appraisal began at the point indicated by no-stimulus responses in the session, and was terminated at the stimulus display.

7. *Inia* are responsive to operant conditioning and do not differ to any significant degree from *Tursiops*.

8. The *Inia* exhibited upside-down swimming, snorting, body flex, and melon wrinkling behaviors as well as extremely quiet breathing at the rate of 1.44 breaths/min.

RECOMMENDATION

Acoustic contamination in the form of bubble accrual on stimulus displays must be accounted for in echolocation studies.

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<p>Echolocation and related behavior in the Amazon River porpoise <i>Inia geoffrensis</i> was investigated to demonstrate biological sonar within the context of operant conditioning. It was found that the <i>Inia</i>'s click train ranged from 25 to 200 kHz; major energy was centered approximately at 100 kHz. The longest periods of silence for the <i>Inia</i> were 8 sec. Corollary behavior exhibited during the performance of the conditioned task indicated a two-step sonic appraisal of the stimulus condition.</p>		

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